Is Whole-Plant Photosynthetic Rate Proportional to Leaf Area? A Test of Scalings and a Logistic Equation by Leaf Demography Census

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ABSTRACT: Allometric scalings and a logistic equation assume that whole-plant photosynthetic rate under resource-unlimited conditions is proportional to leaf area. We tested this proportionality for the herb *Helianthus tuberosus*. During growth, we repeatedly measured the percentage of leaves with high, medium, and low photosynthetic capacity to estimate the whole-plant sum of photosynthetic capacity. We found that the whole-plant sum of the light-saturated photosynthetic rate of leaves is proportional to the whole-plant leaf area, disregarding the dynamics of the leaf population. We also found that the daily photosynthesis of each leaf appeared as a linear function of the light-saturated photosynthetic rate of that leaf, as predicted by the optimization theory. Using those results, we expressed whole-plant photosynthetic rate as a product of the light-saturated whole-plant photosynthetic rate and an efficiency index that reflects resource limitation as in the logistic equation. This efficiency decreased with increasing leaf area, reflecting light limitation. Therefore, realized whole-plant photosynthetic rate is not proportional to leaf area. These "diminishing returns" are well explained by a simple saturating curve, such as the logistic equation.

Keywords: metabolic scaling theory, whole-plant photosynthesis, allometry, leaf demography, logistic equation, *Helianthus tuberosus* (Jerusalem artichoke).

Introduction

Whole-plant photosynthetic rate (P_{plant}) is one of the most important traits under natural selection (Givnish 1982). Allometric scaling models predict P_{plant} as a growth model, in which different-sized plants correspond to plants at different times (t) through ontogeny (West et al. 1999, 2001; Niklas and Enquist 2002; West and Brown 2005). The model consists of two relations. First, whole-plant leaf area at time t ($F_{(t)}$) is predicted to be a power function of whole-plant mass at that time ($M_{(t)}$), so-called allometry (West et al. 1999; Niklas and Enquist 2002):

$$F_{(t)} = Y_0 M_{(t)}^{\theta}, \tag{1}$$

where Y_0 and θ are constants. The second is the assumption that whole-plant photosynthetic rate at time t ($P_{\text{plant}(t)}$) is assumed to be proportional to the whole-plant leaf area, so-called isometry (West et al. 1999; Niklas and Enquist 2002; Enquist et al. 2007*b*):

$$P_{\text{plant}(t)} = BF_{(t)}, \tag{2}$$

where B is constant and independent of $F_{(t)}$. Combining these two, the allometric scaling theory predicts $P_{\text{plant}(t)}$ as a power function of $M_{(t)}$ (Niklas and Enquist 2002). Nevertheless, although mechanisms underling the allometry (eq. [1]) have been provided (West et al. 1999), the mechanism underlying the assumption of isometry (eq. [2]) is unknown.

This assumption neglects increasing resource limitation (Muller-Landau et al. 2006*b*; Enquist et al. 2007*b*). Actual $P_{\text{plant}(t)}$ realized under field conditions should be reduced by resource limitation, such as self-shading with increasing leaf area (e.g., Hirose et al. 1996; Hikosaka et al. 1999; Oikawa et al. 2005). The incorporation of resource limitation into allometric scaling models is needed (Enquist et al. 2007*b*). Here we propose that resource limitation can be incorporated into allometric scalings in the same manner as the logistic equation. The logistic equation is based on the assumption that $P_{\text{plant}(t)}$ is proportional to $F_{(t)}$ only when any resource is unlimited:

$$P_{\text{plant max}(t)} = AF_{(t)}, \tag{3}$$

where $P_{\text{plant max}(t)}$ indicates $P_{\text{plant}(t)}$ under a resource-unlimited condition and A is assumed to be constant, independent of $F_{(t)}$. We refer to this assumption (eq. [3]) as "pro-

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Table 1: List of the important symbols

Symbol	Units	Definition
$c_{(F,\,t)}$	g C m^{-2} s^{-1}	Intercept of $P_{n(l,\,t)}$–$P_{n\,max(l,\,t)}$ linear relation on day t
$\varepsilon_{(F)}$		Efficiency index of whole-plant photosynthetic rate under field conditions with given $F_{(t)}$
$F_{(t)}$	m^2	Whole-plant leaf area on day t
$f_{(l,\,t)}$	m^2	Area of the lth leaf of one plant on day t
l		Leaf position for one plant on day t
$\lambda_{n(F,\,t)}$		Slope of $P_{n(l,\,t)}$–$P_{n\,max(l,\,t)}$ linear relation on day t
$P_{n(l,\,t)}$	g C m^{-2} s^{-1}	Net photosynthetic rate under field conditions for the lth leaf averaged over day t
$P_{n\,max(l,\,t)}$	g C m^{-2} s^{-1}	Light-saturated net photosynthetic rate for the lth leaf on day t
$P_{plant(t)}$	g C s^{-1}	($\equiv \sum_{l=1}^{L} P_{n(l,\,t)} f_{(l,\,t)}$) Whole-plant net photosynthetic rate under field conditions averaged over day t
$P_{plant\,max(t)}$	g C s^{-1}	($\equiv \sum_{l=1}^{L} P_{n\,max(l,\,t)} f_{(l,\,t)}$) Whole-plant light-saturated net photosynthetic rate on day t

portionality in capacity" hereafter. The logistic equation expresses $P_{plant(t)}$ as a product of $P_{plant\,max(t)}$, with an efficiency index ($\varepsilon_{(F)}$) that reflects resource limitation:

$$P_{plant(t)} = \varepsilon_{(F)} P_{plant\,max(t)} = \varepsilon_{(F)} A F_{(t)} = B_{(F)} F_{(t)}. \quad (4)$$

The efficiency $\varepsilon_{(F)}$, called the "available substrate," decreases with increasing leaf area (Pastijn 2006; Thornley and France 2007). By comparing equation (4) and equation (2), it appears that B in the allometric scalings can be partitioned into A and $\varepsilon_{(F)}$ in the logistic equation. Equation (2) is a special case of equation (4), in which both A and $\varepsilon_{(F)}$ are constants. We will ask whether equation (4) has a logical basis, focusing on the following two aspects.

First, A is assumed to be constant in the logistic equation. As we have discussed, allometric scalings also implicitly assume A to be constant. However, leaf population has a dynamic age structure (Bazzaz and Harper 1977). Only in the special cases where leaf numbers are kept constant or where production and shedding of leaves are balanced is age structure expected to be stable (Traw and Ackerly 1995; Ackerly 1999; Kikuzawa 2003). Nevertheless, when total leaf area is increasing during growth, there is no reason to a priori assume a constant age structure, and therefore, detailed study is necessary (Bazzaz and Harper 1977; Hodanova 1981). The importance of age structure for whole-plant photosynthesis has long been recognized by single-leaf-based studies (Bazzaz and Harper 1977; Hodanova 1981; Field 1983; Kitajima et al. 2002; Hikosaka 2003, 2005). Nevertheless, it has been ignored both in the allometric scalings and in the logistic equation. To solve this discrepancy, we will first test the proportionality in capacity for an age-structured leaf population.

Second, the efficiency $\varepsilon_{(F)}$ is the ratio of $P_{plant(t)}$ to $P_{plant\,max(t)}$ on each day during growth. In general, the degree of shading is different from leaf to leaf, requiring leaf-layer-based modeling (i.e., Hirose and Werger 1987; Anten et al. 1995; Pearcy and Yang 1996; Thornley 2002; Hikosaka 2003; Oikawa et al. 2008). Hence, to express $\varepsilon_{(F)}$ by other parameters may be complex. Instead, based on the idea of ecological scaling (Field 1991; Sellers et al. 1992), we will express $\varepsilon_{(F)}$ with a few parameters that are equal among leaves on a single plant in a single given day.

Here we conducted a single-leaf-based investigation (leaf demography census and photosynthesis measurements) during growth of the perennial herb *Helianthus tuberosus*. First, we tested the proportionality in capacity (eq. [3]) for an age-structured leaf population. Second, efficiency $\varepsilon_{(F)}$ was expressed by parameters, all equal within a single plant. Our aim is to solve the discrepancy between single-leaf studies and allometric scaling theories.

Model

The important symbols are listed in table 1. Suppose a plant consists of L leaves. The whole-plant photosynthetic rate under field conditions on day t ($P_{plant(t)}$) is the sum of the photosynthetic rate of all the leaves on a single plant (Bazzaz and Harper 1977):

$$P_{plant(t)} = \sum_{l=1}^{L} P_{n(l,\,t)} f_{(l,\,t)} \quad (5)$$

(g C s^{-1}, averaged over day t); $P_{n(l,\,t)}$ refers to the net photosynthetic rate per unit area of the lth leaf averaged over day t; and $f_{(l,\,t)}$ is the single-leaf area of that leaf. Note that the leaf order l is independently numbered from the stem apex for each day for each plant. We first hypothesized that leaves with different photosynthetic capacities are distributed so as to maximize $P_{plant(t)}$ (Field 1983). This is realized when the gross actual photosynthetic rates of leaves within a plant are proportional to the gross maxi-

mum photosynthetic rates of those leaves (Farquhar 1989; Sellers et al. 1992).

That is, for any leaf l of a single plant on day t,

$$P_{g(l,t)} = \lambda_{g(F,t)} P_{g\max(l,t)} \tag{6}$$

(g C m^{-2} s^{-1}); $P_{g(l,t)}$ refers to the gross photosynthetic rate per unit area of the lth leaf on day t; $P_{g\max(l,t)}$ is the light-saturated gross photosynthetic rate of that leaf; and $\lambda_{g(F,t)}$ is a dimensionless ratio ($0 < \lambda_{g(F,t)} < 1$). Under the optimization hypothesis, $\lambda_{g(F,t)}$ is predicted to be equal within a plant on day t and therefore independent of the leaf position l (Sellers et al. 1992). Note that $\lambda_{g(F,t)}$ may change day by day. The gross photosynthetic rate is the sum of the net photosynthetic rate and the respiration. Therefore, equation (6) can be rewritten as

$$P_{n(l,t)} + R_{(l,t)} = \lambda_{g(F,t)}(P_{n\max(l,t)} + R_{(l,t)}) \tag{7}$$

(g C m^{-2} s^{-1}); $R_{(l,t)}$ (>0) refers to the respiration rate per unit area of the lth leaf. The respiration rate consists of growth and maintenance respirations (Thornley 1970). The former is proportional to net photosynthetic rate, and the latter is proportional to leaf mass per unit area (m; g leaf m^{-2}):

$$R_{(l,t)} = pP_{n(l,t)} + qm \tag{8}$$

(g C m^{-2} s^{-1}); p (>0; dimensionless) and q (>0; g C s^{-1} g^{-1} leaf) are constants. We assume m to be constant, independent of l (Hikosaka 2003). Substitution of equation (8) into equation (7) yields

$$P_{n(l,t)} = \left[\frac{\lambda_{g(F,t)}}{1 + p(1 - \lambda_{g(F,t)})}\right] P_{n\max(l,t)} - qm\left[\frac{1 - \lambda_{g(F,t)}}{1 + p(1 - \lambda_{g(F,t)})}\right] \tag{9}$$

(g C m^{-2} s^{-1}). The resulting formula appears as a linear function of $P_{n\max(l,t)}$. The slope and the intercept of equation (9) are functions of $\lambda_{g(F,t)}$, p, q, and m so that both are independent of l. The intercept is negative because $\lambda_{g(F,t)} < 1$ and $p, q, m > 0$. To simplify, we replace the slope and the intercept of equation (9) with $\lambda_{n(F,t)}$ and $c_{(F,t)}$ (<0), respectively:

$$P_{n(l,t)} = \lambda_{n(F,t)} P_{n\max(l,t)} + c_{(F,t)} \tag{10}$$

(g C m^{-2} s^{-1}). The slope $\lambda_{n(F,t)}$ is a dimensionless ratio. Note that the differentiation of equation (10) with respect to $P_{n\max(l,t)}$ yields the equal-slope λ_n (Field 1991). The assumption of optimization will be tested in this study, but here we proceed to the further analysis based on equation (10). By substituting equation (10) into equation (5), we obtain

$$P_{plant(t)} = \lambda_{n(F,t)}\left[\sum_{l=1}^{L} P_{n\max(l,t)} f_{(l,t)}\right] + c_{(F,t)} F_{(t)} \tag{11}$$

(g C s^{-1}); $\sum_{l=1}^{L} P_{n\max(l,t)} f_{(l,t)}$, the sum of the light-saturated photosynthetic rates of all the leaves on a single plant, is equivalent to $P_{plant(t)}$ under a resource-unlimited condition ($P_{plant\max(t)}$). Therefore, equation (11) can be rewritten as

$$P_{plant(t)} = \lambda_{n(F,t)} P_{plant\max(t)} + c_{(F,t)} F_{(t)} \tag{12}$$

(g C s^{-1}). Here, we assume proportionality in capacity (eq. [3]) before we test it for further analysis. Substitution of equation (3) into the right side of equation (12) yields

$$P_{plant(t)} = AF_{(t)}\left(\lambda_{n(F,t)} + \frac{c_{n(F,t)}}{A}\right) \equiv AF_{(t)}\varepsilon_{(F)} \tag{13}$$

(g C s^{-1}), where

$$\varepsilon_{(F)} \equiv \left(\lambda_{n(F,t)} + \frac{c_{n(F,t)}}{A}\right).$$

The efficiency $\varepsilon_{(F)}$ is a dimensionless ratio. Therefore, under the two conditions of optimization (eq. [10]) and proportionality in capacity (eq. [3]), $\varepsilon_{(F)}$ can be expressed by five physiological parameters ($\lambda_{g(F,t)}$, A, p, q, and m), all of which are independent of leaf position l. The resulting formula is the same expression as the logistic equation (eq. [4]), in which $\varepsilon_{(F)}$ is independent of l.

The efficiency $\varepsilon_{(F)}$ is a function of $\lambda_{g(F,t)}$, with the other four parameters (A, p, q, and m) being constant. It may change day by day because of both internal and external factors. Unlike "substrate" in the logistic equation (Thornley and France 2007), resource availability $\varepsilon_{(F)}$ will not be unity when $F_{(t)} = 0$. This is because even if there is no self-shading, leaves will not be light saturated for 24 h because of the diurnal solar cycle. This $\varepsilon_{(F)}$ in general is a function of day (t) itself, as a result of weather fluctuations. To incorporate light limitation in relation to only plant size, as in the logistic equation, we measured $P_{plant(t)}$ under similar open-sky photosynthetically active radiation (PAR) in the following experiment. Hence, $\varepsilon_{(F)}$ is regarded as a function of only $F_{(t)}$. Because of self-shading with increasing $F_{(t)}$, a negative correlation between $\varepsilon_{(F)}$ and

$F_{(t)}$ is expected. Therefore, even when proportionality in capacity is true, the resulting $P_{\text{plant}(t)}$ is expected to show diminishing returns, unlike isometry in the allometric scalings.

Methods

Study Species

Helianthus tuberosus L. is a naturalized perennial herb introduced from North America (Shimizu 2003). The phyllotaxis is usually opposite. The plants usually grow from tubers in spring and reach more than 2 m. They flower in autumn, and all the aboveground parts die at the beginning of winter.

Growth Conditions

The study site is the experimental farm of Ishikawa Prefectural University (36°30′N, 136°35′E, 39 m a.s.l.) in Nonoichi, Japan. Mean annual temperature and mean annual precipitation are 14.6°C and 2,337 mm, respectively (2002–2006; data from IPU-1, Ishikawa Prefectural University). In December 2006, tubers were taken from the adjacent field. Twenty-five healthy medium-sized tubers were planted at a 1-m^2 plot (5 × 5 rows with 20-cm spacing) in an open place. A total of 40 stems (one to four stems per tuber) germinated from late April to early May in 2007. All except one of them grew quite well. During the study, the stems of the inner layer did not elongate their lateral branches. We use the word "plant" for each stem hereafter.

Leaf Demography Census

Three plants (labeled A–C) were continuously monitored. The aboveground parts of the three plants emerged during the period from April 27 to April 30, 2007. Each leaf was identified, and its survival was monitored at 1–8-day intervals from stem emergence until July 31. Our study period from May to July is included in the "grand period of growth" (Hunt 1990), when total leaf number increased continuously and when the flower buds had not yet differentiated. During the study, new leaves appeared successively from the apical meristem on the stem, and the oldest leaves fell successively at the base of the stem. At each time of observation, leaves that had newly achieved full expansion were counted until they were shed. For at least one leaf on each pair of opposite leaves, leaf length was measured when they were newly counted. Leaf areas were calculated with the area-length regression, obtained from destructive sampling after the study. For the opposite leaves on the same nodes, the same leaf areas were applied. Only the interior tubers were used to avoid edge effects. The three plants grew quite similarly in terms of total leaf area and height. The heights of the plants reached 1.5 m at the end of the study.

The relative position ($F_{\text{above}(l,t)}/F_{(t)}$) of each leaf on each plant is defined as the cumulative leaf area on that plant above that leaf ($F_{\text{above}(l,t)}$) divided by the whole-plant leaf area ($F_{(t)}$) on day t (Hirose and Werger 1987). All the stems were vertical. The uppermost leaf at the top of the stem has $F_{\text{above}(l,t)}/F_{(t)} = 0$ and the lowermost leaf has $F_{\text{above}(l,t)}/F_{(t)} = 1$.

Measurement of Photosynthetic Rate

For each of the three plants (A–C), one leaf at every node was measured in situ for net light-saturated photosynthetic rates ($P_{\text{n max}(l,t)}$) by using a portable infrared gas analyzer (LI-6400, LI-COR, Lincoln, NE) with 1- or 2-week intervals (for details, see appendix in the online edition of the *American Naturalist*).

The relation between realized daily averaged net photosynthetic rate under natural-light condition of one leaf on one day ($P_{\text{n}(l,t)}$) and $P_{\text{n max}(l,t)}$ of that leaf on that day was obtained five times with 2-week intervals from May 28 to July 24. All of those days were sunny with thin clouds, and the daily averaged open-sky PARs were similar (fig. 1). Each day, nine to 15 leaves from one to five plants were measured. As the plants became larger, leaves from fewer plants were measured to ensure that leaves from the entire range of positions were measured. Gas exchange rates and incident PAR under natural light for each leaf were repeatedly measured six to eight times each day, in-

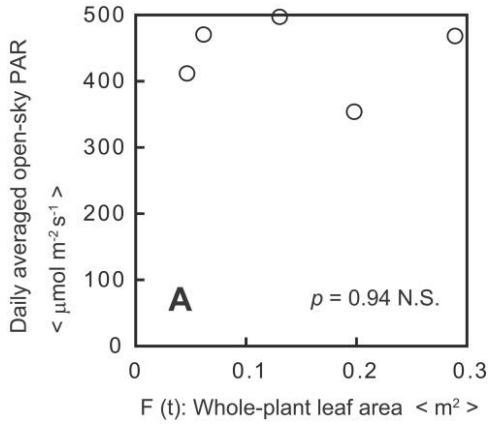

Figure 1: Daily averaged open-sky photosynthetically active radiation (PAR) on each of the 5 days, in relation to mean whole-plant leaf area of the three monitored plants on that day ($F_{(t)}$). No significant correlation exists between them. Each circle indicates one measurement day.

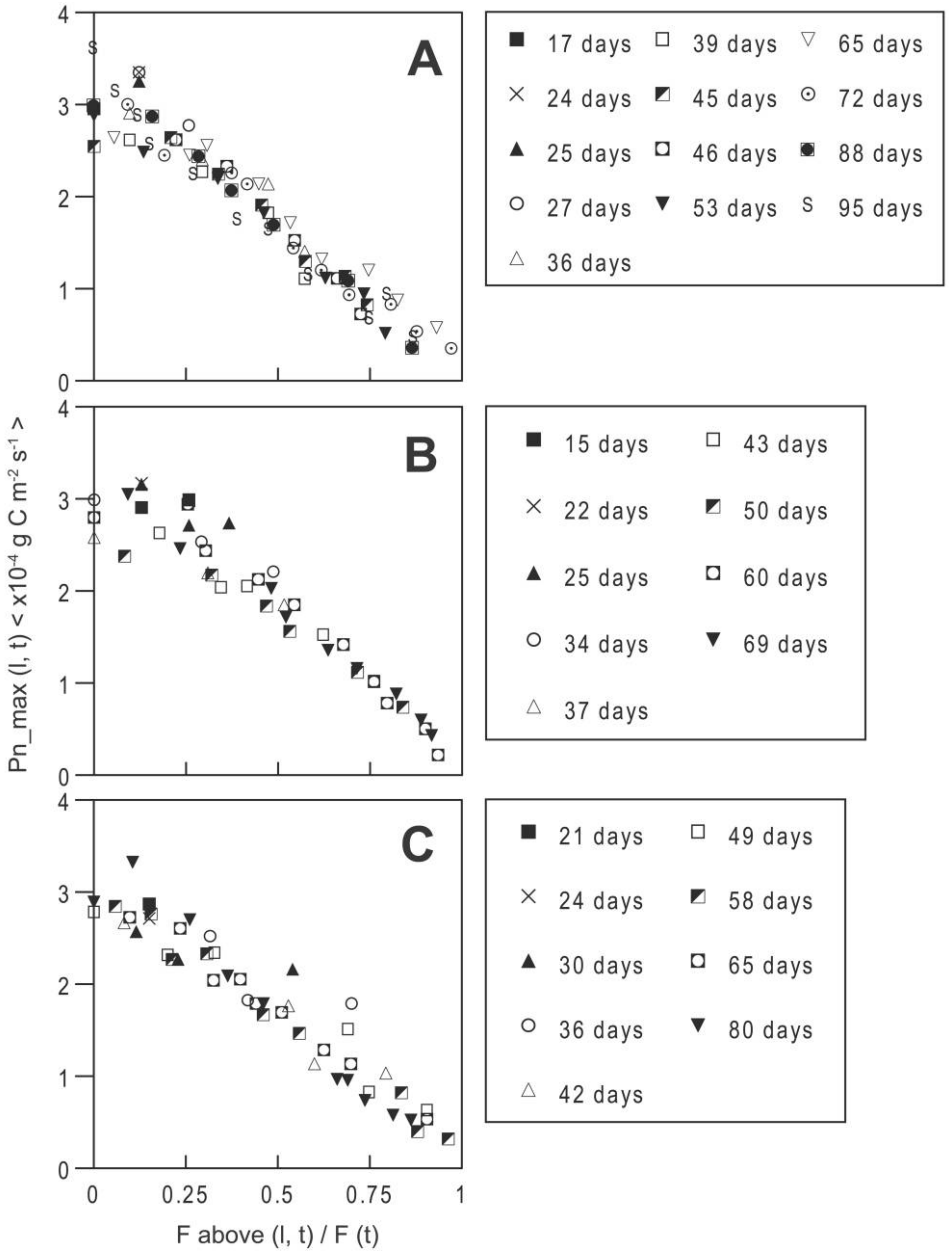

Figure 2: Light-saturated net photosynthetic rate of each leaf on each day ($P_{\mathrm{n\,max}(l,t)}$) in relation to relative position on each plant on that day ($F_{\mathrm{above}(l,t)}/F_{(t)}$; i.e., 0 = top, 1 = bottom). Each panel shows one plant (plants A–C). Each symbol indicates one leaf measured on each day. Days from the emergence of each plant are shown.

cluding two dark-respiration measurements at dawn and sunset (for details, see appendix). All the statistics in this study were calculated using SPSS 13.0J for Windows.

Results

Intraplant Distribution of $P_{n\,max(l,\,t)}$

At any point during growth, the youngest leaves just after their full expansion showed the highest $P_{\mathrm{n\,max}(l,t)}$, around 2.6–3.6 × 10^{-4} g C m^{-2} s^{-1} (=22–30 μmol m^{-2} s^{-1}); $P_{\mathrm{n\,max}(l,t)}$ declined almost linearly from the top to the bottom of the plants. During growth, a leaf with a similar relative position ($F_{\mathrm{above}(l,t)}/F_{(t)}$) on each day had similar $P_{\mathrm{n\,max}(l,t)}$ (fig. 2). We fitted a different linear regression of $P_{\mathrm{n\,max}(l,t)}$ on $F_{\mathrm{above}(l,t)}/F_{(t)}$ for each plant on each day in which more than three leaves were measured ($r^2 > 0.89$, $p <$ .05 for all lines). The lines were not obtained for the earliest

days, in which fewer than four leaves near the stem apex were measured (see appendix). The slopes and the intercepts of those lines do not significantly differ within each plant (for the three plants, slope: $p = .18$–$.32$; ANCOVA: $p = .19$–$.92$), except for only one line (80 days of plant C). The slope on this day for that plant was significantly different from the rest of the days ($p = .04$). With the exception of this line, the slopes and the intercepts of those lines do not significantly differ among all the lines from all three plants (slope: $p = .07$; ANCOVA: $p = .30$).

Proportionality in Capacity

Using the fitted $P_{\mathrm{n}\max(l,t)} - (F_{\mathrm{above}(l,t)}/F_{(t)})$ linear regressions, we estimated the $P_{\mathrm{n}\max(l,t)}$ of all the leaves on each plant. The estimated $P_{\mathrm{plant}\max(t)}$ ($=\Sigma P_{\mathrm{n}\max(l,t)} f_{(l,t)}$) for each day was proportional to the $F_{(t)}$ for that day (fig. 3). The proportionality in capacity is supported. The slopes and the intercepts do not significantly differ among the plants (slope: $p = .08$; ANCOVA: $p = .11$). Using equation (3), we then calculated A for each plant as the slope of the line set through the origin. Because the intercepts of those lines are virtually 0, setting through the origins only slightly (<4%) changes the value of the slopes.

Relation between $P_{n(l,t)}$ *and* $P_{n\ max(l,t)}$

The daily time course of CO_2 exchange rates basically follows incident PAR on the leaves. We did not observe any visible midday depressions on any of the 5 days (data not shown). A fairly linear relation between $P_{\mathrm{n}(l,t)}$ and $P_{\mathrm{n}\max(l,t)}$ was observed (fig. 4). These slopes and intercepts of the $P_{\mathrm{n}(l,t)}$–$P_{\mathrm{n}\max(l,t)}$ lines correspond to $\lambda_{\mathrm{n}(F,t)}$ and $c_{(F,t)}$ in equation (10) for each day. All the intercepts were negative, as predicted. Because of the limited sample size, we pooled all the leaves from all the measured plants within each day and calculated $\lambda_{\mathrm{n}(F,t)}$ and $c_{(F,t)}$, and these values are commonly applied to all three plants. Positive correlation between $P_{\mathrm{n}(l,t)}$ and daily averaged PAR on that leaf was significant ($r^2 = 0.85$–0.96, $p < 1.0 \times 10^{-5}$), except the earliest measurement day of the 5 days (i.e., 30 days from stem emergence; $r^2 = 0.30$, $p = .08$). Relative PAR on the leaves (i.e., mean daily averaged PAR on the measured leaves divided by daily averaged open-sky PAR) on each day was negatively correlated with the whole-plant leaf area (averaged over the three monitored plants) on that day ($r^2 = 0.79$, $p < .05$).

Whole-Plant Daily Photosynthesis

The efficiency index ($\varepsilon_{(F,t)}$) and whole-plant photosynthetic rate ($P_{\mathrm{plant}(t)}$) were calculated with equation (13) for the 5 days. As expected, negative correlation between $\varepsilon_{(F,t)}$ and $F_{(t)}$ was found ($r^2 > 0.806$, $p < .05$ for the three plants). Hence, the relation between $P_{\mathrm{plant}(t)}$ and $F_{(t)}$ was explained by a convex quadratic curve (fig. 5).

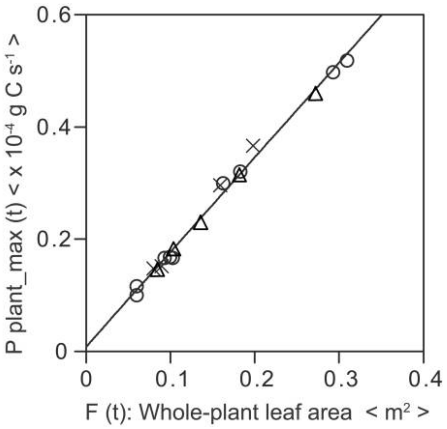

Figure 3: Light-saturated whole-plant photosynthetic rate on each day ($P_{\mathrm{plant}\max(t)}$) in relation to whole-plant leaf area on that day ($F_{(t)}$). Each series of symbols indicates one plant: *circles*, plant A ($n = 9$); *crosses*, plant B ($n = 4$); and *triangles*, plant C ($n = 5$); $P_{\mathrm{plant}\max(t)}$ was not obtained for the earliest days, in which only one to three leaves on the upper part of the stems were measured. Linear regression for each plant is significant ($r^2 > 0.995$, $p < .01$ for all plants). The line on the graph indicates regression through the entire data set ($r^2 > 0.993$, $p < 1.0 \times 10^{-18}$, $n = 18$), and its intercept is not significantly different from 0 ($p = .18$): $P_{\mathrm{plant}\max(t)} = 8.19 \times 10^{-7} + 1.69 \times 10^{-4} F_{(t)}$.

Discussion

Structure of Leaf Population

Leaf population has a dynamic age structure. Nevertheless, proportionality in capacity (eq. [3]) was proven during growth (fig. 3). This is because leaf population structure, in terms of photosynthetic capacity, did not change largely during growth (fig. 2). Therefore, $P_{\mathrm{n}\max(l,t)}$ averaged over a plant did not change during growth (i.e., affine translation from small to large leaf population, "affine model"). This result has a discrepancy with previous studies conducted in dense stands, which reported that plants made their leaf nitrogen (and $P_{\mathrm{n}\max(l,t)}$) distribution steeper in a denser stand than in a less dense stand (Hirose et al. 1988, 1989, 1997; Schieving et al. 1992). Nevertheless, there are also several reports with no significant effects of increased self-shading on intraplant nitrogen gradients or photosynthesis (Hirose et al. 1988; Ackerly and Bazzaz 1995). Those studies indicate that the change in the leaf population size does not always have a large effect on $P_{\mathrm{plant}\max(t)}$, except in dense stands. For dense stands, the change in the intraplant distribution of $P_{\mathrm{n}\max(l,t)}$ may impose another effect. Also, in the very initial period, there

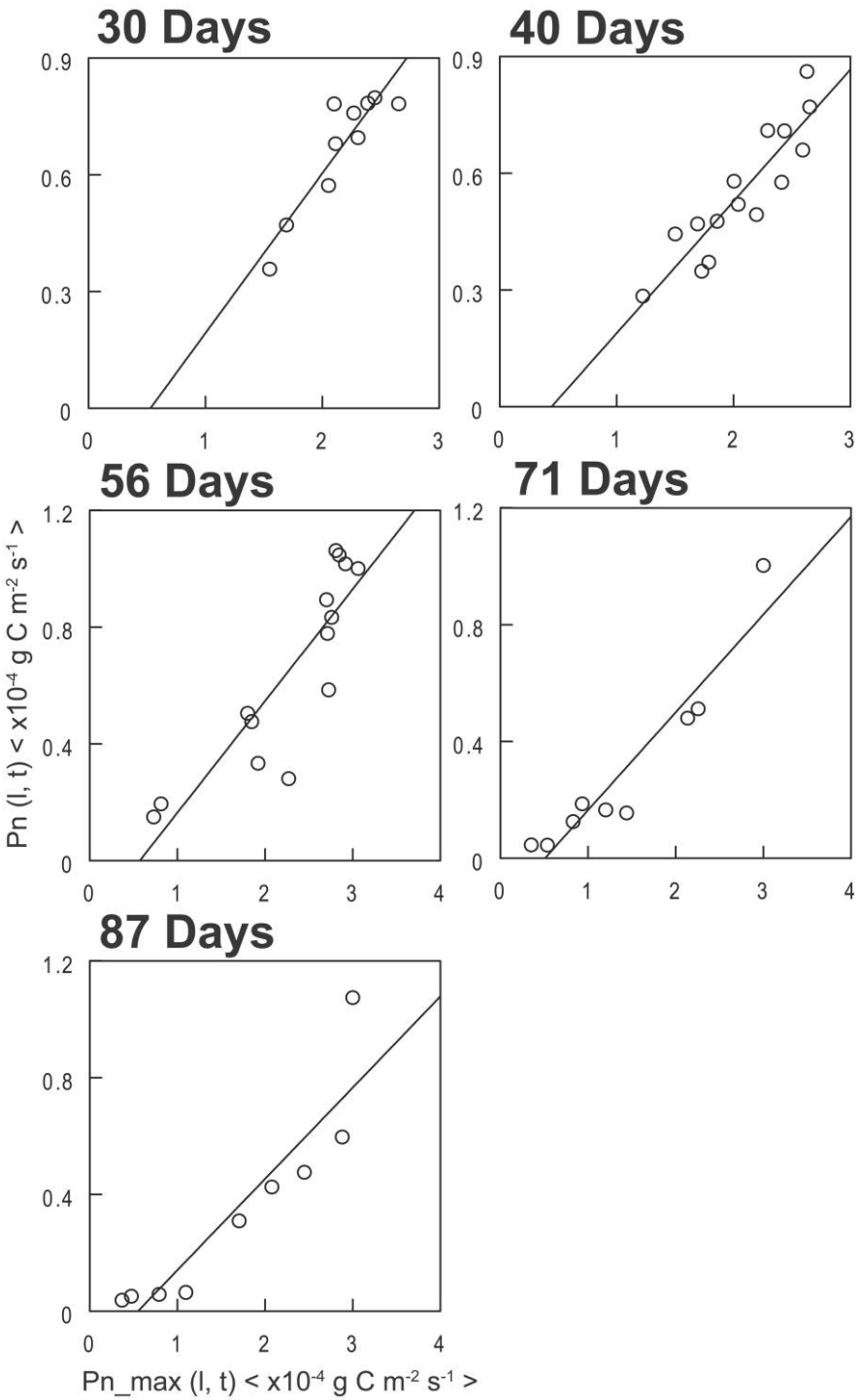

Figure 4: Photosynthetic rate under field conditions of one leaf averaged over each day ($P_{n(l,t)}$) in relation to light-saturated net photosynthetic rate of that leaf on that day ($P_{n\max(l,t)}$). Each panel shows one measurement day and days from the mean plant emergence day (April 28). Each circle indicates a single leaf. All the regression lines are significant ($r^2 = 0.76$–0.90, $p < .001$): 30 days, $P_{n(l,t)} = -2.17 \times 10^{-5} + 0.411P_{n\max(l,t)}$; 40 days, $P_{n(l,t)} = -1.50 \times 10^{-5} + 0.339P_{n\max(l,t)}$; 56 days, $P_{n(l,t)} = -2.19 \times 10^{-5} + 0.383P_{n\max(l,t)}$; 71 days, $P_{n(l,t)} = -1.71 \times 10^{-5} + 0.335P_{n\max(l,t)}$; 87 days, $P_{n(l,t)} = -1.72 \times 10^{-5} + 0.313P_{n\max(l,t)}$.

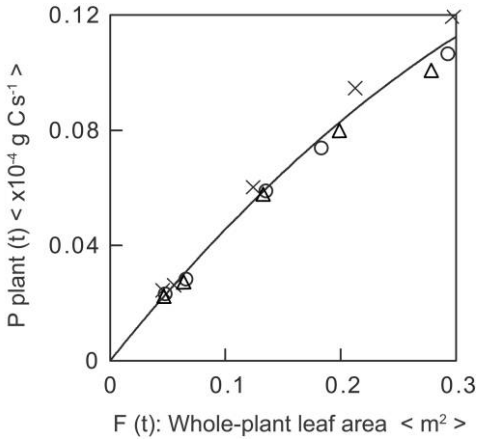

Figure 5: Whole-plant net photosynthetic rate under field conditions averaged over each of the 5 days ($P_{\text{plant}(t)}$) in relation to whole-plant leaf area on that day ($F_{(t)}$). Each series of symbols indicates one plant (*circles*, plant A; *crosses*, plant B; *triangles*, plant C). Quadratic regression for each plant is significant ($r^2 > 0.998$, $p < .01$ for all plants). The curve on the graph shows quadratic regression through the entire data set ($r^2 = 0.986$, $p < 1.0 \times 10^{-11}$), and its intercept is not significantly different from 0 ($p = .99$): $P_{\text{plant}(t)} = 7.39 \times 10^{-9} + 4.95 \times 10^{-5} F_{(t)} - 4.02 \times 10^{-5} F_{(t)}^2$.

are only young leaves on the stem, so the gradient changes naturally (see Hodanova 1981). From this, we could expect that the constancy of the gradient starts from the beginning of the shedding of the lowermost leaves. A plant is known to start shedding leaves before the light level of its lowermost leaf drops under the compensation point, unless surplus nitrogen is supplied (Oikawa et al. 2006, 2008). Our leaf census data showed that the plants started shedding in the early period at 27–33 days, when total leaf area was still increasing. Therefore, our result is not confined to the period after the canopy is closed. Overall, our results are consistent with reports of growth analysis indicating that net assimilation rate is fairly constant during vegetative growth when self-shading is small (Heath 1938; Hunt and Evans 1980; Hirose 1984). Furthermore, our result (proportionality in capacity) explains the initial exponential growth of a plant (Blackman 1919; Gregory 1921), which is universally observed for plants under resource-unlimited conditions. To our knowledge, this is the first study to explain the exponential growth of a plant with an age-structured leaf population.

Whole-Plant Daily Photosynthetic Rate

As predicted by the optimization hypothesis (eq. [10]), the daily net photosynthetic rate of each leaf is expressed as a linear function of the net light-saturated photosynthetic rate of that leaf on day t with negative intercepts (fig. 4). Actual canopy structure is often suboptimal rather than optimal (Pons et al. 1989). Game theory successfully explains the discrepancy between optimal and suboptimal structures (Givnish 1982; Anten 2005). Hence, severe competition may also change the simple relation.

Available PAR for each leaf decreased as the plants grew, as a result of increased self-shading. Positive correlation between PAR on each leaf and daily photosynthetic rate of that leaf indicates that light was a limiting resource. The decline of the efficiency index ($\varepsilon_{(F)}$) with increased $F_{(t)}$ reflects increased self-shading. Combining the proportionality in capacity (fig. 3) and the decline of $\varepsilon_{(F,t)}$, we found that the relation between $P_{\text{plant}(t)}$ and $F_{(t)}$ was explained by the saturating curve, such as the convex quadratic (fig. 5), as in the logistic equation (Thornley and France 2007). It showed diminishing returns rather than the assumption of proportionality between $P_{\text{plant}(t)}$ and $F_{(t)}$ in the allometric scalings (eq. [2]). When we express $P_{\text{plant}(t)}$ (g C s^{-1}) as a power function of $F_{(t)}$ (m^2; i.e., $P_{\text{plant}(t)} = aF_{(t)}^b$), we obtain $a = 3.33 \times 10^{-5}$ and $b = 0.875$ ($r^2 = 0.983$, $p < 1.0 \times 10^{-13}$) for the data pooled from the three plants. The exponents appear <1.

In general, $F_{(t)}$ scales as a power function of whole-plant mass (eq. [1]), in which θ refers to the scaling exponent. Allometric scaling models predict that $\theta = 1$ for small plants (herbs/saplings) and $\theta = 3/4$ for large trees (Enquist et al. 2007*a*, 2007*b*), though there are many controversies for these scaling exponents (e.g., Chen and Li 2003; Muller-Landau et al. 2006*a*, 2006*b*; Reich et al. 2006, 2007). Our model can be incorporated into these allometric scaling theories. The allometry between whole-plant leaf mass and whole-plant mass (Shinozaki et al. 1964; West et al. 1999; Niklas and Enquist 2002; Enquist et al. 2007*a*, 2007*b*) and between leaf area and leaf mass (Reich 2001; Milla and Reich 2007; Niklas et al. 2007; Price and Enquist 2007) is still valid. Only the assumption of proportionality between $P_{\text{plant}(t)}$ and $F_{(t)}$ should be revised to incorporate resource availability. By estimating $F_{(t)}$ from those allometric relations, $P_{\text{plant}(t)}$ can be calculated as another function of $F_{(t)}$. Various growth functions (see review in Thornley and France 2007) combined with the ecological scalings (Field 1991; Sellers et al. 1992) will provide the relation between $P_{\text{plant}(t)}$ and $F_{(t)}$. The logistic equation (i.e., quadratic of $F_{(t)}$) is an example that seems to be suitable to the present case.

The relation between $P_{\text{plant}(t)}$, $P_{\text{plant max}(t)}$, and $F_{(t)}$ can be explained by a simple relation if and only if the external factors are constant. Forest species experience a different light regime through ontogeny (Brienen and Zuidema 2006; Muller-Landau et al. 2006*b*; Poorter 2007), and different-sized forest plants often show different leaf traits as an acclimation to this (Reich et al. 2004; Koyama and Kikuzawa 2008). Therefore, variation of external environment through ontogeny will affect both $P_{\text{plant max}(t)}$ and

$\varepsilon_{(F)}$. Water stress also changes the normal allometry (Chen and Li 2003). Therefore, it is natural to doubt whether simple relations exist across different habitats (cf. Chen and Li 2003; Muller-Landau et al. 2006*a*, 2006*b*; Reich et al. 2006, 2007). However, those site-specific factors can occur simultaneously with the intrinsic ones. Even when intrinsic behaviors of plants follow simple rules across all situations or habitats (e.g., Blackman 1919; Field 1991; West and Brown 2005), the extrinsic factors may often be prevalent, resulting in the absence of a consistent trend across all habitats (cf. Chen and Li 2003; Muller-Landau et al. 2006*a*, 2006*b*; Reich et al. 2006, 2007). That prevalence of extrinsic factors does not preclude the validity of the intrinsic ones. Applicability and limitation of the scaling theories will be clarified, and then further development will be possible, only if the relation between whole-plant photosynthetic rate and single leaf physiology is revealed.

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Appendix from K. Koyama and K. Kikuzawa, "Is Whole-Plant Photosynthetic Rate Proportional to Leaf Area? A Test of Scalings and a Logistic Equation by Leaf Demography Census"

(Am. Nat., vol. 173, no. 5, p. 640)

Methods of Photosynthesis Measurements

Measurement of Leaf Photosynthetic Capacity

The measurement started 2–3 weeks after the emergence of the aboveground parts. This is the time when the uppermost leaves reach a height of 8 cm from the ground, which was determined by the size of the measuring chamber. In the earliest days, only leaves near the stem apex were measured. Because of successive shedding of the lowermost leaves, the leaves in all positions become measurable. For each plant, one leaf at every node was measured. Each time, leaves that had newly achieved full expansion were added to the sample, and the same leaf samples were continuously measured thereafter until their lamina turned yellow. Leaves that were damaged severely by herbivory were not measured for photosynthesis. In the early days, all of the leaf samples from the three plants were measured on the same days. As sample size increased, one or two plants were measured each day in turn. Because of this, the total number of measurements, as well as the dates of the last measurements, differ among the three plants. The measurements ended 69–95 days after the plants' emergences, which was the end of the rainy season, and 1 or 2 months before the appearance of inflorescences. We finished our measurement earlier than the expected end of the grand period of growth. This was because air temperature at the site frequently exceeded 33°C once the rainy season had ended, so heat stress seemed not to be negligible.

Net light-saturated photosynthetic rate of each of those leaves in each day ($P_{\mathrm{n\,max}(l,t)}$) was measured under photosynthetically active radiation (PAR) 2,000 μmol m^{-2} s^{-1}, supplied with an LED light source inside the leaf chamber. In preliminary experiments, the species showed higher photosynthetic rates under 2,000 μmol m^{-2} s^{-1} than under lower PAR (K. Koyama and K. Kikuzawa, unpublished data). The CO_2 concentrations inside the chamber were controlled at 350 μmol mol^{-1} air. Air temperature was at ambient conditions and ranged from 22° to 33°C, except on one day when it rose to 35°C. Measurements were conducted between 7:30 and 11:30 a.m. The plants were watered to saturation in the evenings before measurement days.

Measurement of Daily Photosynthesis

Gas exchange rates of each leaf were repeatedly measured six to eight times each day, including two dark-respiration measurements at dawn and sunset. On each occasion, the incident PAR on those leaves was measured with a quantum sensor (IKS-27, KOITO, Yokohama, Japan) set on the leaves with a measuring bar with the same inclination as the leaves. PAR on all the leaves was measured within 20 min each time. Next, the instantaneous net photosynthetic rates of those leaves at that moment were measured using an LI-6400 under the same light levels just obtained, supplied with the LED light source; $P_{\mathrm{n\,max}(l,t)}$ of those leaves was measured with PAR 2,000 μmol m^{-2} s^{-1} in the morning. Dark respiration rates at dawn and sunset for each leaf were used as predawn and postsunset nighttime respiration rates for each day. For all the above measurements, the air temperature was at ambient conditions, and CO_2 concentrations inside the chamber were maintained at 350 μmol mol^{-1} air. Daily averaged net photosynthetic rate of each leaf on each day ($P_{\mathrm{n}(l,t)}$) was obtained by interpolating those instantaneous values over each day. Daily averaged open-sky PAR on each day was measured by another quantum sensor set on a 2-m pole near the plot. The plants were watered to saturation in the evenings before measurement days.

The above $P_{\mathrm{n}\max(l,t)}$ data in the daily photosynthesis measurements contain days in which leaves from the entire position of plant A were measured. As these measurements of $P_{\mathrm{n}\max(l,t)}$ were conducted with identical methods (e.g., time of day, ambient temperature range, supply of water before the measurements, etc.), we incorporated these $P_{\mathrm{n}\max(l,t)}$ data into the data described above.